

A new tillodont from the early Middle Eocene of Japan and its implication to the subfamily Trogosinae (Tillodontia : Mammalia)

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Received 28 September ; Revised manuscript accepted 16 February 1998

Abstract. A new large tillodont, represented by a fragmentary right mandible with M/2-3, was found in the upper part of the Akasaki Formation, the early Middle Eocene of Japan. It is the first record of the order Tillodontia in Japan, and is described as a new genus and species, *Higotherium hypsodon*, of the subfamily Trogosinae. It resembles the North American forms *Trogosus* and *Tillodon* in size ; however it apparently differs from those and *Kuanchuanius* from China in having more hypsodont molars with well developed cusps. In detailed comparison with other trogosine molars, this new tillodont is one of the most derived taxa of the order, and morphologically situated in between the above three genera and the genus *Chungchienia* known from China, which was recently reassigned to the order. Morphological differences among these genera, including *Higotherium hypsodon*, indicate that the new taxon shows a closer relationship with *Chungchienia* than with North American genera, and that the rapid evolutionary diversification of the Trogosinae occurred before and during the Middle Eocene.

Key words : Akasaki Formation, early Middle Eocene, *Higotherium*, phylogenetic relationships, Tillodontia, Trogosinae

Introduction

Tillodonts are extinct herbivorous mammals having elongated I2/2, and are known from the Paleocene to Eocene strata in North America, Europe, and Asia. The order Tillodontia Marsh, 1875, which was systematically revised by Gazin (1953), includes a single family Esthonychidae Cope, 1883, that is divided into two subfamilies : Esthonychinae and Trogosinae, based mainly on the morphology of I2/2. Although various authors have discussed tillodont origins and phylogenetic relationships with the mammalian orders Pantodonta (e.g., Chow and Wang, 1979 ; Muizon and Marshall, 1992 ; Lucas, 1993) and Anagalida (Ting and Zheng, 1989), the oldest and most primitive tillodonts are known only from the early to middle Paleocene of China (Ting and Zheng, 1989). The occurrences of the earliest tillodonts in China suggest that their ancestor originated in Asia, and that tillodonts then migrated into North America and Europe via Beringia during the Late Paleocene to Middle Eocene (Gingerich and Gunnell, 1979 ; Stucky and Krishtalka, 1983 ; Krause and Maas, 1990 ; Baudry, 1992 ; Chow *et al.*, 1996).

The subfamily Trogosinae hitherto included four genera : *Trogosus* Leidy, 1871 and *Tillodon* Gazin, 1953 from North America, and *Kuanchuanius* Chow, 1963a and *Chungchienia* Chow, 1963b from China (see Chow *et al.*, 1996). The first three genera are known from the late Early to early Middle Eocene, based on recent chronological and biostratigraphical studies (Krishtalka *et al.*, 1987 ; Tong, 1989 ; Prothero, 1995). Chow *et al.* (1996) systematically revised the taxonomic position of *Chungchienia*, known from the middle Eocene, and concluded that it is the most derived genus of Trogosinae. The subfamily Trogosinae, established by Gazin (1953), is characterized by having many derived characters : elongated rootless I2/2 with labial enamel band, more hypsodont molars than those of esthonychines, massive skull, and deep mandible with well developed symphysis. Although tillodont material is never plentiful, several phylogenetic hypotheses regarding the Tillodontia have recently been proposed by Stucky and Krishtalka (1983), Baudry (1992), Lucas (1993), and Chow *et al.* (1996). Their cladograms suggest that the trogosine tillodonts are phylogenetically situated in the most derived monophyletic group within the order, whereas the Esthynchinae are no

longer a monophyletic group.

Eocene mammals have seldom been found in Japan, and the new tillodont described below is the oldest known mammalian fossil from the Tertiary of Japan. Although remains of the new tillodont do not include the diagnostic incisors, it certainly belongs to the subfamily Trogosinae based on the cusp patterns of hypsodont molars and its large size. This paper adds a new taxon from Japan to Trogosinae, and focuses on the phylogenetic position and affinities between North American and Asian trogosines.

The following institutional abbreviations are used in this paper: **AMNH**, American Museum of Natural History, New York, New York; **ANSP**, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, People's Republic of China; **NMC**, Canadian Museum of Nature, Ottawa, Canada (formerly the National Museums of Canada); **NSM**, Department of Geology, National Science Museum, Shinjuku, Tokyo, Japan; **USNM**, National Museum of Natural History, Washington, D. C.; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Geological setting and the age of Akasaki Formation

The locality of the tillodont specimen described below is located on the coast at Akasemachi, Uto Peninsula, about 15 km west of Uto City, Kumamoto Prefecture, Japan (Figure 1). The specimen was found in the gray-blue siltstone belonging to the upper part of the Akasaki Formation. The Akasaki Formation belongs to the Miroku Group of Nagao (1926) or the Akasaki Group of Matsushita (1949); it is the basal unit of the Paleogene strata distributed in the western part of Uto Peninsula and Amakusa area. The Paleogene strata are widely distributed in the area and unconformably overlie the Upper Cretaceous Himenoura Group. The Paleogene stratigraphy was established by Nagao (1926), who divided it into three Groups: the Miroku, Hondo, and Sakasegawa Groups in ascending order (Figure 1). After his work, several stratigraphic nomenclature revisions of the Paleogene strata have been proposed by other authors, and their stratigraphic schemes and detailed stratigraphy are summarized by Miki (1972, 1975).

The Akasaki Formation is composed of nonmarine fluvial sediments; it consists largely of red siltstone, gray-blue siltstone, and conglomerate. This formation is approximately 400m in thickness at Uto Peninsula, but unrecognized in

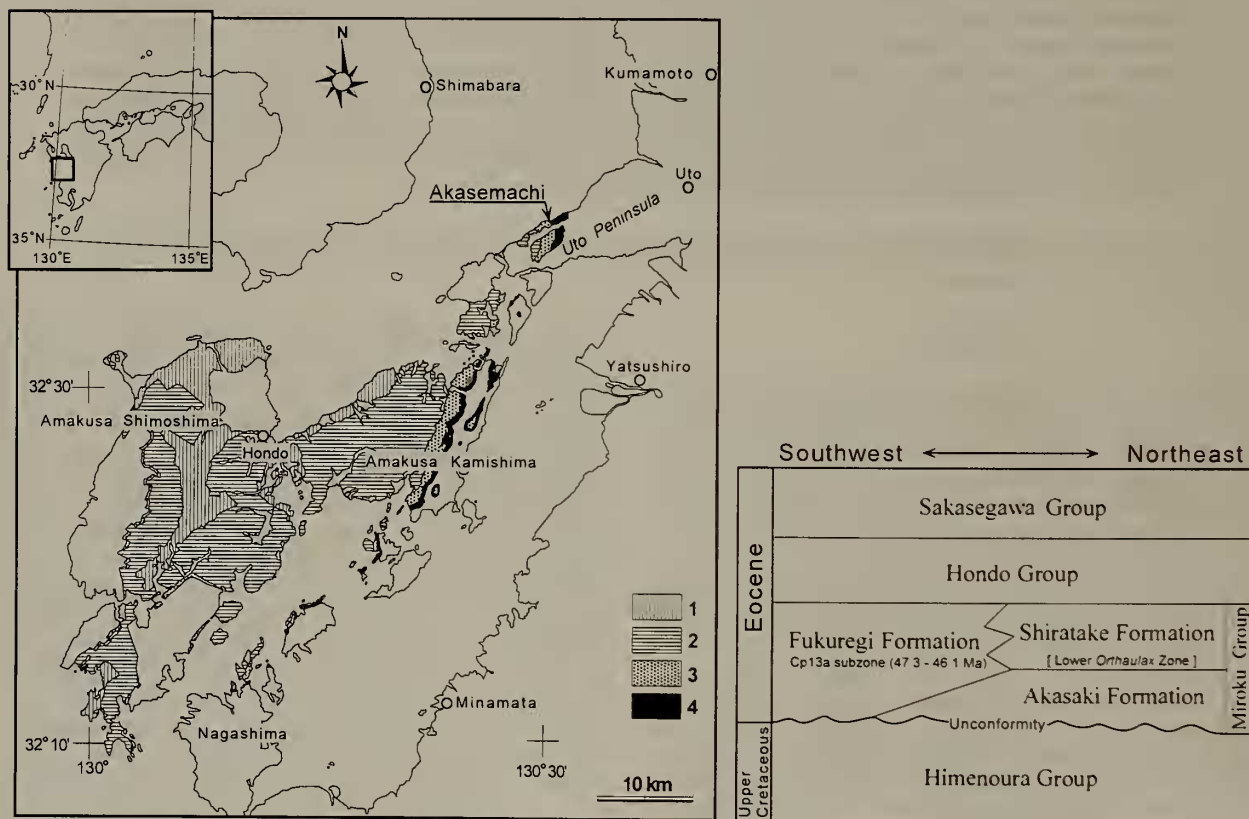


Figure 1. Left, Geological sketch map showing the fossil locality (Akasemachi), Amakusa area and Uto Peninsula, western part of Kyushu, Japan (modified from Miki, 1975). 1: Sakasegawa Group, 2: Hondo Group, 3: Shiratake and Fukuregi Formations, 4: Akasaki Formation. Right, stratigraphic relationships of the Paleogene strata distributed in the area.

the Amakusa Shimoshima, and has hitherto been unfossiliferous. Because no reliable fossil evidence has been found in the Akasaki Formation, the geologic age of the Akasaki Formation has been discussed by various authors (e.g., Miki, 1975; Takai and Satoh, 1982; Miki and Matsueda, 1985) based mainly on stratigraphic correlation with the conformably overlying strata: the Fukuregi and Shiratake Formations (see also Figure 1) which include marine invertebrate fossils. The Shiratake Formation, distributed in the eastern part of Amakusa area and Uto Peninsula, consists mainly of shallow marine sediments and yields abundant molluscan fossils near the basal part. The molluscan fossiliferous horizon was named "Lower *Orthaulax* Zone" by Nagao (1926), and is widely traceable in the area. The Shiratake Formation is generally correlated with the Fukuregi Formation based on the lithofacies and similar molluscan fauna (Miki, 1972, 1975). The Fukuregi Formation, which is another basal unit of the Paleogene strata distributed in the Amakusa Shimoshima, bears larger foraminifera such as *Nummulites* and *Discocyclina* in addition to the molluscan fossils. The *Nummulites*-bearing rocks of the Fukuregi Formation and the Lower *Orthaulax* Zone of the Shiratake Formation are regarded as the same fossiliferous horizon, and both were previously considered Ypresian (Early Eocene) in age on the basis of the *Nummulites* and molluscan fossils (Hanzawa and Urata, 1964; Miki, 1975). Consequently, Miki and Matsueda (1985) referred to the previous interpretation of the Paleogene stratigraphy, and estimated the geological time range of the Akasaki Formation as Middle Paleocene to Early Eocene based on their preliminary work on the magnetostratigraphy of this formation.

However, the previous biostratigraphic interpretation from the molluscan fauna and *Nummulites* is not supported by data from the nannoflora from the Fukuregi Formation (Tashiro *et al.*, 1980). Recently, Okada (1992) reported on the nannofossil zones of the Paleogene distributed in the western part of Kyushu, and reassigned the nannoflora of the Fukuregi Formation to the Cp13a subzone (approximately 47.3–46.1 Ma, Berggren *et al.*, 1995, p. 194), the early Middle Eocene. Therefore, the geologic age of the Lower *Orthaulax* Zone, previously assigned to the Early Eocene as mentioned above, is also more likely placed in the early Middle Eocene on the basis of Okada's (1992) conclusion. The horizon of the new tillodont is situated at about 18 m below the Lower *Orthaulax* Zone. Although the geologic age of the lower limit of the Akasaki Formation has not been resolved, the gray-blue siltstone that yielded the tillodont fossil is probably the same age, early Middle Eocene, without any great time gap.

Systematic paleontology

Order Tillodontia Marsh, 1875
 Family Esthonychidae Cope, 1883
 Subfamily Trogosinae Gazin, 1953
 Genus *Higotherium* gen. nov.

Type species.—*Higotherium hypsodon* sp. nov.

Diagnosis.—Size similar to those of *Tillodon* and *Trogosus*,

but smaller than that of *Chungchienia*, and much larger than that of *Kuanchuanius*. Lower molars much more hypsodont than those of *Tillodon*, *Trogosus*, and *Kuanchuanius*, with well developed cusps. The buccal crowns not so distinctly tapering upward as in *Tillodon*, and not so markedly convex in transverse section as in *Trogosus*. M/3 has an elongated large metaconid and anteroposteriorly shortened third lobe which displays a deep, enclosed basin; M/3 also has two additional small cusps, namely a mesoconid on the cristid obliqua and a cusp on the paracristid.

Etymology.—From Higo, an ancient name of present Kumamoto Prefecture, plus *therium* (Gr.), beast.

Higotherium hypsodon sp. nov.

Figures 2–4

Holotype.—A right mandible fragment with M/2 and M/3, NSM-PV 20118.

Type locality.—Coast at Akasemachi, Uto City, Kumamoto Pref., Japan (Figure 1).

Horizon.—The upper part of the Akasaki Formation (approximately 18 m below the Lower *Orthaulax* Zone).

Age.—Most likely early Middle Eocene.

Etymology.—From *hypsos* (Gr.), high, plus *odon* (Gr.), tooth, referring to its hypsodont molars.

Diagnosis.—Same as for the genus until other species may be found.

Description

Terminology of molar structures mostly follows that of Bown and Kraus (1979), and extra terms are indicated in Figure 3A.

Mandible: The anterior portion of mandible (anterior to M/2) and the distal ends of the coronoid, condyle, and angular processes are missing. In addition, the mandibular ramus is weakly laterally compressed. However, the remaining portion of mandible is well-preserved, and the outline of the missing portion is faintly preserved as a weak impression on the matrix. The length of the complete mandible is estimated to have been approximately 30 cm, judging from the impression and the size of the remaining portion. The mandible is massive and deepest in the area between M/2 and M/3. The masseteric fossa, extending between coronoid and condyle processes, is deeply concave at the anterior portion of mandibular ramus. The anterior margin of the mandibular ramus is subvertical relative to the occlusal surface of the tooth row (the angle of about 80°), and rises behind the M/3 talonid (Figure 2).

Lower molars: The lower molars are extremely hypsodont on the buccal side in contrast to the appearance of the lingual side, as in other tillodonts. The buccal wall is columnar with a narrow and deep hypoflexid between the trigonid and talonid, while the lingual wall is almost flattened (Figure 3B). The cristid obliqua is very strong and links to the posterolingual wall of the protocristid near the base of the metaconid as in other trogosines. The enamel surface on the buccal side is entirely rugose with longitudinal, weak

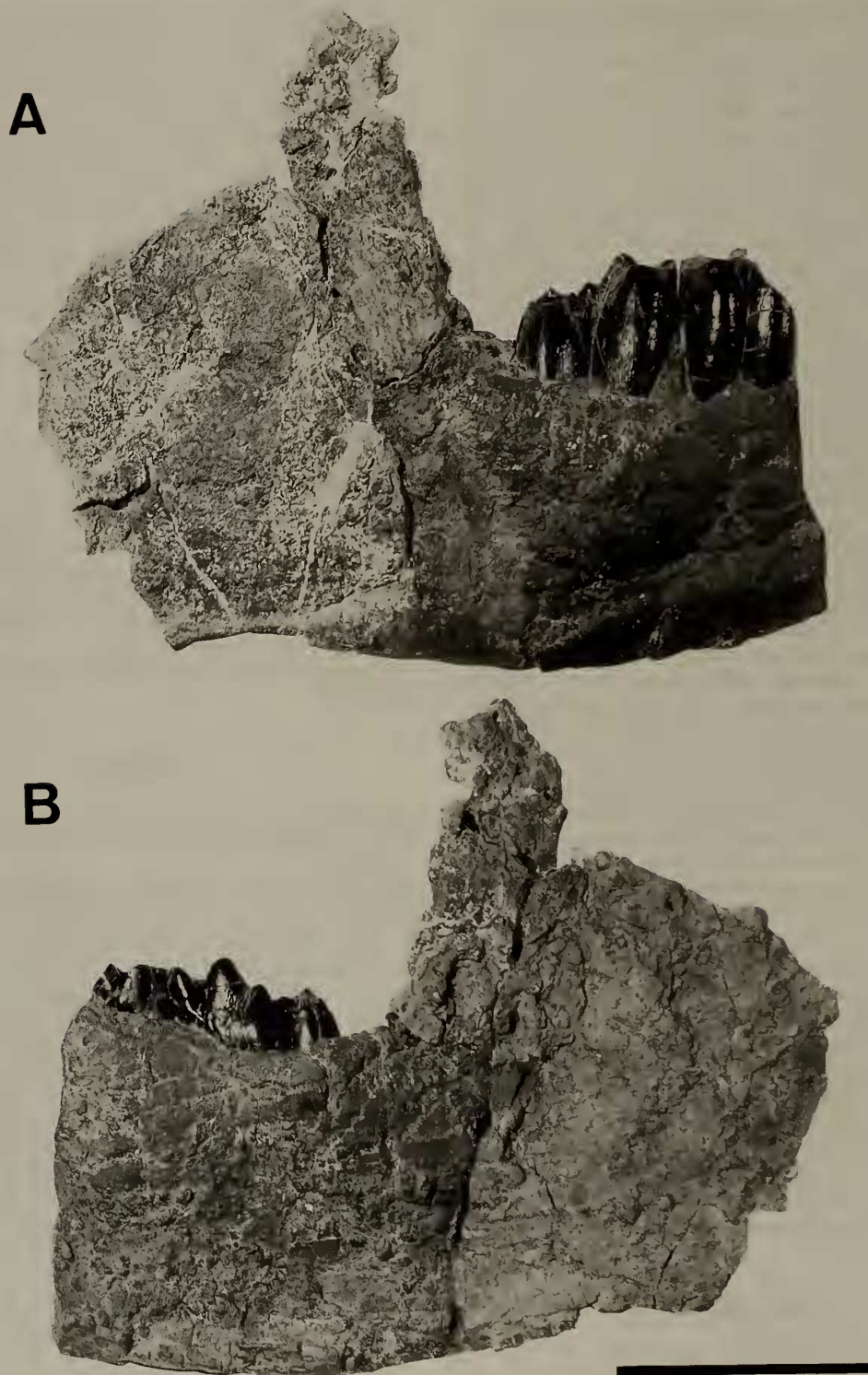


Figure 2. *Higotherium hypsodon* gen. et sp. nov. Holotype : NSM-PV 20118, right fragmentary mandible with M/2 and M/3. A : buccal view, B : lingual view. Scale bar equals 5 cm.

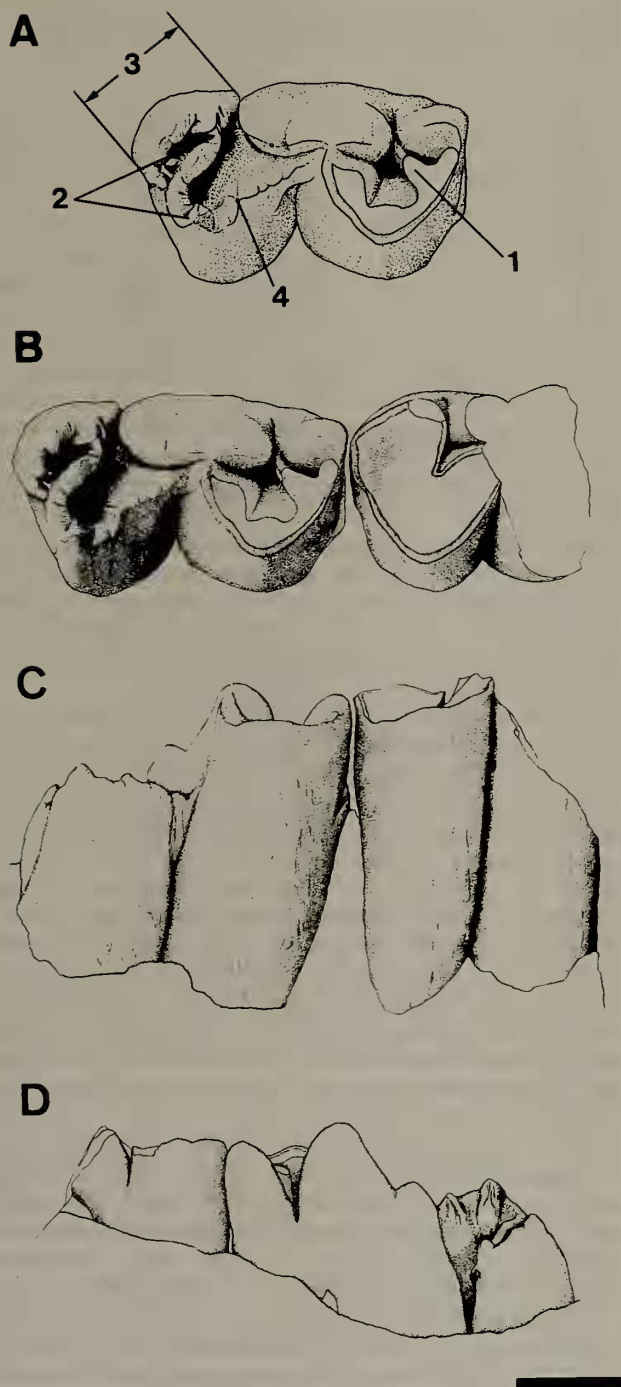


Figure 3. Right M/2 and M/3 of *Higotherium hypsodon* gen. et sp. nov. Holotype: NSM-PV 20118. **A:** positions of extra cusps and ridges on the M/3 discussed in the text, 1: an additional cusp on the paracristid, 2: posthypocristid, 3: third lobe, 4: mesoconid. **B:** occlusal view, **C:** buccal view, **D:** lingual view. Scale bar equals 1 cm.



Figure 4. Lingual radiograph of right M/2 and M/3 of *Higotherium hypsodon* gen. et sp. nov. Holotype: NSM-PV 20118. Scale bar equals 2 cm.

lines, that are absent on the lingual side (Figures 3C and D). The cervical line is unexposed above the dentary in both molars (Figure 3C). Although soft X-ray photographs of NSM-PV 20118 were taken in order to examine the development of the molar roots, it could not be determined whether the roots were formed or not. However, it is clear that both molars extend deep in the dentary (Figure 4), and thus they are quite hypsodont.

M/2: Most of the M/2 trigonid was missing when collected, hence cusps of the trigonid are unknown. Width of the trigonid is almost equal to that of the talonid (Table 1), and the trigonid is slightly shorter anteroposteriorly than that of M/3, judged by the remaining part of the crown. The buccal wall of the talonid is slightly bowed toward the occlusal surface in posterior view, and the buccal margin of the talonid exhibits a swollen V-shape in horizontal cross section. The posterior portion of the metaconid is distinctly elongated, but detailed structure of the metastylid is mostly unknown since its apex is not preserved. The entoconid, hypoconulid, and hypoconid have lost much of their details by heavy wear. Two ridges extend from the hypoconid: the cristid obliqua anterolingually and a ridge joining to the hypoconulid posterolingually; and the hypoconulid is further connected with the entoconid by another ridge (i.e., postcristid). All three ridges are very strong and broad. The talonid notch between the entoconid and metastylid is narrow and deep. The cristid obliqua becomes narrower anteriorly and is separated from the metastylid by a narrow notch. This narrow notch steeply descends posteriorly and joins with the

Table 1. Measurements (in mm) of mandible and lower molars of NSM-PV 20118, holotype of *Higotherium hypsodon* gen. et sp. nov. Asterisk (*) indicates measurement of damaged tooth.

Mandible	
Internal maximum depth, between M/2 and M/3	67.8
Maximum thickness, under M/2	25.3
Lower molars	
M/2 Length	20.8*
Width of trigonid	17.5
Width of talonid	18.1
M/3 Length	35.4
Width of trigonid	20.5
Width of talonid	19.5
Width of third lobe	10.5

talonid notch.

M/3: M/3 is an almost unworn tooth in contrast to the heavily worn M/2 (Figure 3B). Width of the trigonid and talonid are nearly equal to those of M/2 (Table 1). In horizontal cross section, the outlines of the buccal margin of both trigonid and talonid are swollen V-shape as in M/2. The buccal wall of the talonid slightly tapers upward. The trigonid basin notch between the paraconid and metaconid is deep and narrow lingually; its bottom is situated slightly lower than that of the M/2 talonid notch at the eruptional stage. The paraconid is sloping and swollen posteriorly; it is slightly constricted at the base of the lingual side. The metaconid is the highest and largest cusp, with the apex slightly curved posteriorly. The posterior arm of the metaconid markedly protrudes from the posterior wall of the protocristid (Figures 3B and C). A prominent metastylid is located on the posterior slope of the metaconid. The paracristid and protocristid extend to the apices of the paraconid and metaconid, respectively. An additional small cusp exists on the paracristid close to the paraconid; it displays a distinct protuberance into the trigonid basin by wear (1 in Figure 3A). A narrow but sharp precingulid is present on the anterior wall of the trigonid (Figures 3B and C).

The M/3 talonid is highly specialized. The talonid basin notch which separates the metastylid from the entoconid displays a lingually opened fissure (Figure 3D). The hypoconid and entoconid are united by a strong ridge (i.e., posthypocristid, 2 in Figure 3A), which separates the primary talonid basin anteriorly and third lobe basin posteriorly, as in *Trogosus grangeri* (see also comparisons section). The third lobe (3 in Figure 3A) is anteroposteriorly shortened, and slightly inclined anteriorly; it shows an oval shape parallel to the cristid obliqua in horizontal cross section. The third lobe also displays a deep enclosed basin which is surrounded by the entoconid, posthypocristid, and a ridge with unidentified cusps (Figure 3B). The posterobuccal wall of the entoconid swells into the third lobe basin. The cristid obliqua becomes narrower dorsally and is separated from the metastylid by a narrow notch that joins the talonid notch as in M/2. A minute but distinct mesoconid exists on the cristid obliqua (4 in Figure 3A); lingual walls of both

hypoconid and mesoconid swell into the talonid basin.

Comparisons

Gazin (1953) divided the Esthonychidae into two subfamilies, Esthonychinae and Trogosinae, based principally on the morphology of I2/2. Although the I2/2 are absent in NSM-PV 20118, *Higotherium hypsodon* certainly belongs to the Trogosinae based on the following characters: much larger size, particularly deep mandible, more hypsodont molars with cristid obliqua close to metaconid, and developed M/3 third lobe basin with a posthypocristid. *Higotherium* is sufficiently distinguished from all other trogosines by many characters as mentioned below. The main comparative measurements and characters discussed in the text are shown in Tables 2 and 3, respectively; and the comparisons were made with original specimens, plus illustrations and descriptions in the literature (Gazin, 1953; Robinson, 1966; Chow, 1963a, b; Chow et al., 1996). Detailed comparisons with North American trogosines that focus on cusps are difficult because the cheek teeth are heavily worn in almost all specimens. Thus, comparisons are based primarily on the specimens having best-preserved crowns among known specimens as shown in Figures 5 and 6.

***Trogosus* Leidy, 1871:** Gazin (1953) recognized five species in the genus *Trogosus*: *T. castoridens* (type species), *T. hyracoides*, *T. grangeri*, *T. hillsii*, and *T. latidens*. The last species was previously questionable and was defined only by its very large size, but was later regarded as a valid species (Stucky and Krishtalka, 1983; Gunnell et al., 1992). Gazin also recognized two structural types among these species: the "long-faced" species (*T. grangeri* and *T. hyracoides*) and "short-faced" species (*T. hillsii* and *T. castoridens*), which probably indicated sexual dimorphism: *T. grangeri* and *T. hyracoides* are related to *T. hillsii* and *T. castoridens*, respectively (Gazin, 1953, p. 40). Although the sexual dimorphic relationships have never been demonstrated, Robinson (1966) believes that *T. hillsii* is probably synonymous with *T. grangeri*.

The mandible of NSM-PV 20118 differs from those of the holotypes of *T. castoridens* (ANSP 10337, AMNH 15590: cast of holotype) and *T. hillsii* (USNM 17157) in having greater depth, a more vertical ascending ramus, and a posteriorly extending masseteric fossa (Table 3). The mandible of NSM-PV 20118 is slightly deeper than those of the holotype of *T. grangeri* (AMNH 17008) and of the specimen (USNM 17886) referred to *T. hyracoides* by Gazin (1953). The M/2-3 of NSM-PV 20118 are slightly larger than those of almost all specimens of *Trogosus* (Tables 1 and 2), and are nearly equal to those of the largest specimen of *T. grangeri* (YPM 16449, examined by Robinson, 1966). Lower molars of *Trogosus* are rather hypsodont, but much less than those of *Higotherium hypsodon*. In fact, the height of the M/2 crown exceeds twice the height of YPM 16449 despite being at nearly the same wear stage (Figures 3C and 5B), and the trigonid and talonid notches, particularly in M/3, are much deeper and narrower in *H. hypsodon*. Gazin (1953, p. 35) noted as a diagnostic feature of *Trogosus* that the buccal walls of lower molars are distinctly convex in transverse

Table 2. Measurements (in mm) of the lower molars of trogosine tillodonts discussed in the text. Asterisks (*) indicate measurements of damaged tooth. The measurements of NMC 8709 and IVPP V 10805 are from Gazin (1953) and Chow et al. (1996), respectively.

Species and catalogue no.	M/1L	M/1W	M/2L	M/2W	M/3L	M/3W
<i>Trogosus grangeri</i> :						
AMNH 17008 (holotype)	14.8	13.8	18.6	15.8	28.8	15.8
AMNH 17009	16.0	13.8	20.0	15.5	31.2	15.5
AMNH 17495A	20.1	15.6*	25.3*	18.2	38.8*	15.0
YPM 16449	20.3	16.4*	21.9	17.5	38.6	18.4
<i>Trogosus hyracoides</i> :						
AMNH 18982	18.0	15.3	20.6	17.2	31.3	15.3
USNM 17886	15.5	14.3	19.8	17.1	27.2	17.6
<i>Trogosus castoridens</i> :						
AMNH 15590 (cast of ANSP 10337 : holotype)	13.5	13.2	19.6	18.0	25.7	12.4
<i>Trogosus cf. castoridens</i> :						
USNM 18165					29.2	16.3*
<i>Trogosus hillsii</i> :						
USNM 17157 (holotype)	15.7	13.4	19.3	14.5	29.8	15.6
<i>Trogosus latidens</i> :						
NMC 8709	20.5		26.3			
<i>Tillodon fodiens</i> :						
YPM 11087 (holotype)	17.2	15.5*	20.9	21.1	35.4	19.4
USNM 18164	16.0	16.6	21.7	19.7*	37.4	19.1
<i>Kuanchuanianus shantunensis</i> :						
IVPP V 2764 (holotype)			19.4	14.9	26.5*	13.3
<i>Chungchienia lushia</i> :						
IVPP V 10805 (holotype)	24	24	28	26	43	22

section, whereas the buccal walls of NSM-PV 20118 are columnar, only slightly convex. All individual cusps of *Trogosus* molars, especially the M/3 metaconid, are less developed than those of *H. hypsodon*. Detailed features of the M/2 entoconid and hypoconulid are also unknown in both YPM 16449 and NSM-PV 20118, but in the latter the postcristid is stronger and wider (Figures 3B and 6B). Moreover, in *Trogosus* the M/3 entoconid is apparently separated from the hypoconulid by a small notch at the unworn stage, whereas in NSM-PV 20118 the M/3 hypoconulid portion is specialized and more strongly connects with the entoconid. In addition, precingulids are apparently reduced or lost in all specimens of *Trogosus* including YPM 16449. Although the presence on M/3 of a mesoconid and an additional cusp on the paracristid cannot be easily assessed in almost all *Trogosus* specimens, the latter accessory cusp is probably absent in *Trogosus* based on our examination of YPM 16449.

In general, the M/3 third lobe of *Trogosus* is elongated posteriorly as in YPM 16449 (Table 2), whereas in NSM-PV 20118 the lobe is much shortened anteroposteriorly and located much more lingually. However, except for the differences of the molar elongation and cusp position, *H. hypsodon* is similar to YPM 16449 in having the same structure on M/3: the talonid is divided into two basins by a strong posthypocristid (Figures 3B and 6B). According to Gazin (1953, p. 44), the divided M/3 talonid basin is a distinctive character of the "Huerfano specimens" of

Trogosus (*T. grangeri* and *T. hillsii*) from the Huerfano Formation, Colorado. Robinson (1966) also recognized the peculiar character of M/3 of the Huerfano *Trogosus*. As Gazin (1953, p. 38) mentioned, in *T. hyracoides* the M/3 talonid basin is little divided or undivided; actually the entoconid and hypoconid are not directly united to each other by a posthypocristid on the left M/3 of AMNH 18982 (Figure 6A, examined by Gazin, 1953), but these two cusps on the right M/3 are slightly connected by a low and narrow posthypocristid based on our careful reexamination. Moreover, a distinct protuberance is present on the buccal side of the left M/3 third lobe in AMNH 18982 (Figures 5A and 6A), but this condition is rarely observed in other *Trogosus* specimens.

Tillodon Gazin, 1953: *Tillodon* is a monotypic genus including *Tillodon fodiens* (Marsh, 1875). *T. fodiens* was previously regarded as the most derived tillodont; it possesses an enlarged skull with somewhat broad and long rostrum, deepened mandible with well developed angular process, a long diastema between P/2 and P/3, loss of I/1 and I/3, less molariform P/4, and a narrower and shorter M3/ than M2/. The known specimens referred to this species are very few: YPM 11087 (holotype), USNM 18164, and USNM 17158 (hypotypes examined by Gazin, 1953).

Higotherium hypsodon is comparable to *Tillodon fodiens* in size (Table 2), and the depth of mandible of NSM-PV 20118 is almost equal to that of YPM 11087 and USNM 18164. However, in *Tillodon* the deepest part of the mandible is not clear, since the ventral edge of the mandible is really parallel

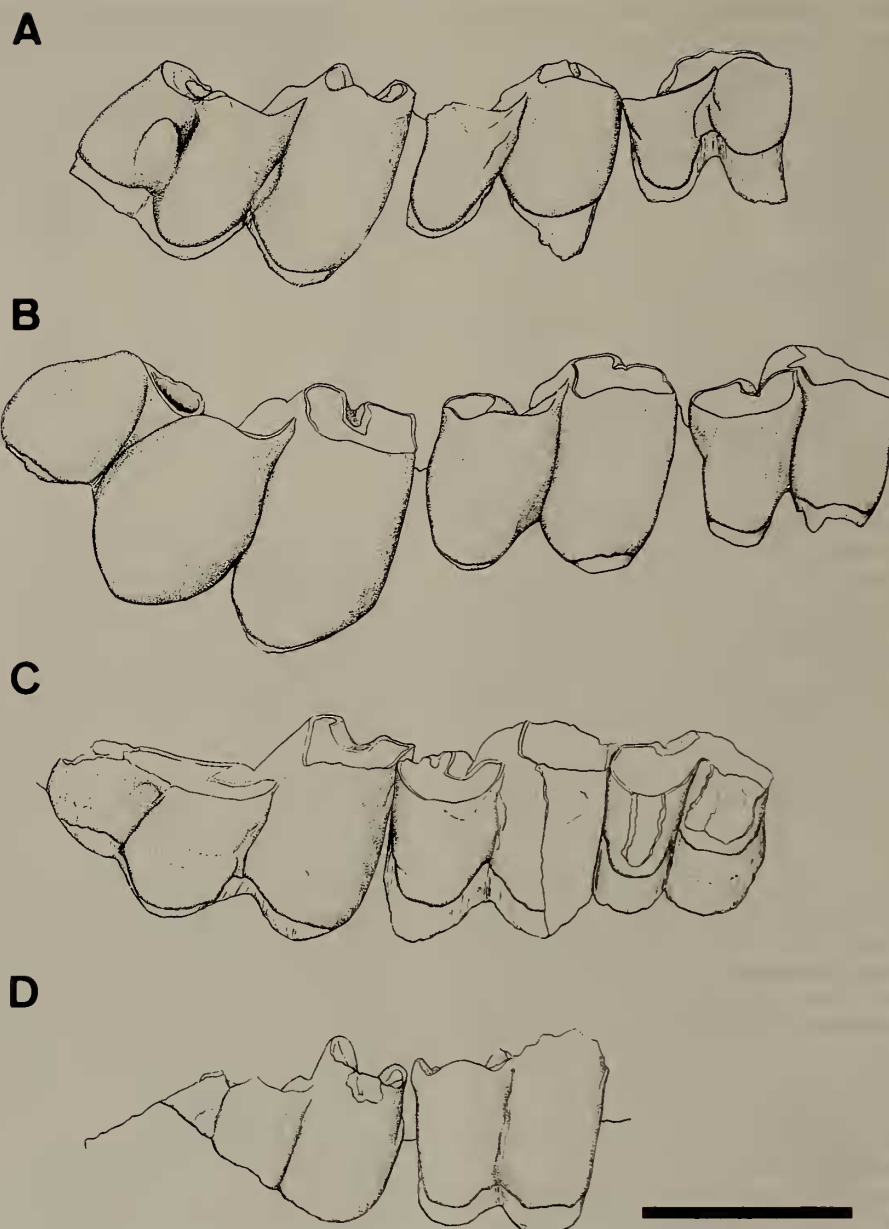


Figure 5. Sketches of well preserved lower molars of trogosines in buccal view. **A:** *Trogosus hyracoides* (AMNH 18982, reversed), **B:** *Trogosus grangeri* (YPM 16449), **C:** *Tillodon fodiens* (USNM 18164), **D:** *Kuanchuanus shantunensis* (holotype: IVPP V 2764). Scale bar equals 2 cm.

to the tooth row. The lower molars of NSM-PV 20118 are much more hypsodont than those of *T. fodiens*, which is distinguished from other trogosines by having brachydont molars despite its large body size (Table 2 and Figure 5C). As Gazin (1953, p. 49) pointed out, in *Tillodon* the buccal walls of the lower molars distinctly taper upward and are externally convex at the base (Figure 5C). Moreover in the lower cheek tooth row of *Tillodon*, the tooth size apparently increases posteriorly (Table 2); the lower molars are tightly arrayed to each other with no space between the teeth; and

the transverse width in M/3 decreases posteriorly (Figure 6C). These features are unlike those of *H. hypsodon*. On the basis of our examination of USNM 18164, all individual cusps on the molars are bulbous in *Tillodon*. The M/3 metaconid of USNM 18164 is relatively low; its posterior slope never protrudes posteriorly from the posterior wall of the protocristid as in NSM-PV 20118 (Figures 3B and 6C). A marked difference is loss of the M/3 metastylid in USNM 18164. A precingulid and a cusp on the paracristid are also absent in the M/3 of *Tillodon*, but these conditions are

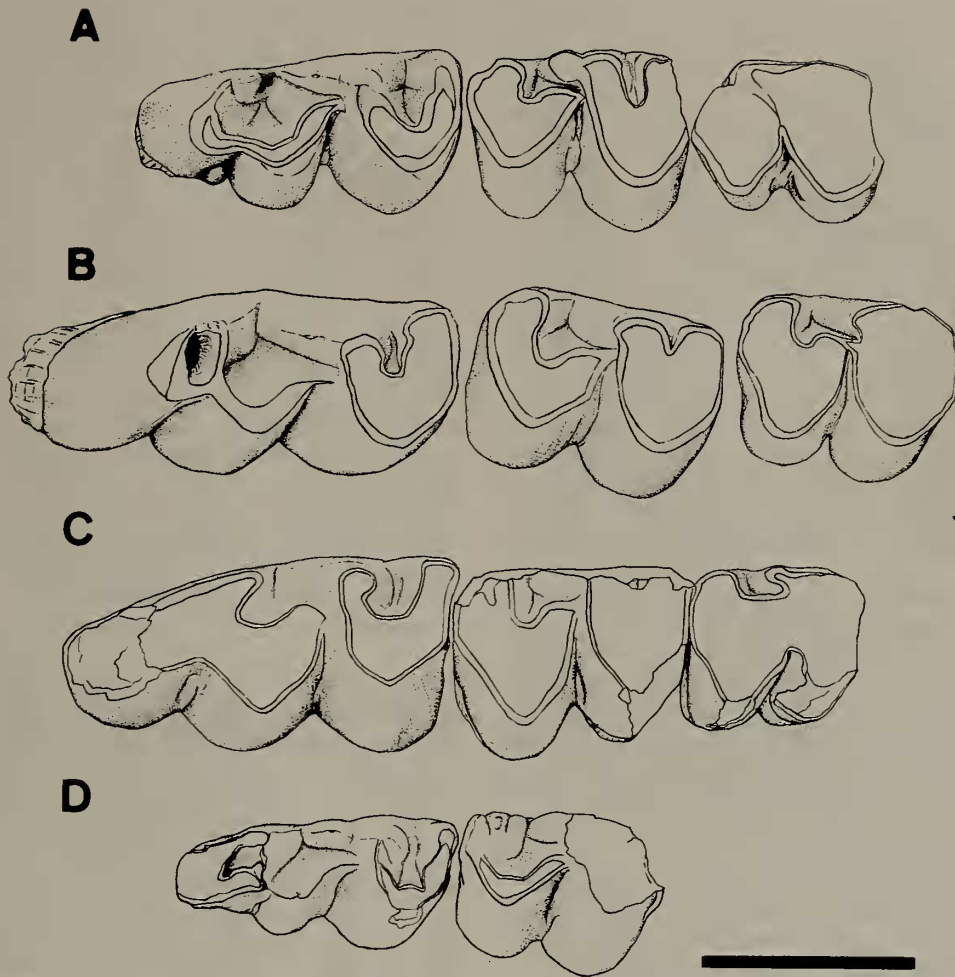


Figure 6. Sketches of well preserved lower molars of trogosines in occlusal view. **A:** *Trogosus hyracoides* (AMNH 18982, reversed), **B:** *Trogosus grangeri* (YPM 16449), **C:** *Tillodon fodiens* (USNM 18164), **D:** *Kuanchuanianus shantunensis* (holotype: IVPP V 2764). Scale bar equals 2 cm.

unfortunately indeterminate in the holotype (YPM 11087) because of heavy wear. The presence of a mesoconid on M/3 is also not observable on either YPM 11087 and USNM 18164, owing to wear. However, the M/3 third lobe of NSM-PV 20118 obviously differs from that of USNM 18164; USNM 18164 has a broad occlusal area of the M/3 talonid with a much elongated entocristid anteroposteriorly (Figure 6C).

***Kuanchuanianus* Chow, 1963:** *Kuanchuanianus* includes two species: *K. shantunensis* Chow, 1963a (type species) and a questionable species, *K. ? danjiangensis* Cheng and Ma, 1990. The former is known by fragmentary mandibles with right and left I/2, right M/2 and M/3 (IVPP V 2764, holotype), and the latter only by an isolated left M/1. Although Chow (1963a) never specified that this Chinese genus belongs to the subfamily Trogosinae, various authors have recognized the morphological similarities between *Kuanchuanianus* and *Trogosus* (Rose, 1972; Stucky and Krishtalka, 1983; Lucas 1993).

Higotherium hypsodon is much larger than *K. shantun-*

ensis; the mandible of IVPP V 2764 is about 40 percent shallower than that of NSM-PV 20118 when compared with the greatest depth. The mandible of IVPP V 2764 is considerably more slender and shorter among known trogosine specimens, and is similar to the holotypes of *T. castoridens* (ANSP 10337) and of *T. hillsii* (USNM 17157) in having shallow depth, a short diastema between P/2 and P/3, anteriorly extending masseteric fossa, and lower angle of the ascending ramus (Table 3). The M/2-3 of *K. shantunensis* are much less hypsodont than those of *H. hypsodon* and are narrower in width relative to other trogosine specimens (Table 2). The two molars of IVPP V 2764 show features clearly because they are almost unworn in spite of their eruption, although a part of the M/2 trigonid and a posterior portion of the M/3 third lobe are broken off. In IVPP V 2764, the M/2 trigonid is much wider than the talonid; M/3 becomes narrower posteriorly; the hypoflexid on M/2-3 is relatively wide; the M/3 third lobe is posteriorly elongated; and the M/2 buccal wall is distinctly convex, as in *Trogosus*,

Table 3. Comparative table of mandibular and lower dental characters among trogosines discussed in the text. 1: *T. hyracoides* and *T. grangeri* (long-faced species), 2: *T. castoridens* and *T. hillsii* (short-faced species), 3: *T. grangeri*, 4: *T. hyracoides*. Question marks (?) indicate not observable.

Mandibular characters	Trogonus				Kuanchuanius		Higotherium		Chungchienia	
	Trogosus	Tillodon	Deep (1) or shallow (2)	Deep	Shallow	Anterior margin of M/1	Deep	?	Extremely deep	?
Depth of mandible	Deep (1) or shallow (2)	Deep	P/4 talonid or M/1	P/4 talonid or M/1 talonid						
Posterior extension of symphysis	Behind (1) or under M/3 talonid (2)	Behind M/3 talonid								
Anterior extension of masseteric fossa	ca. 70° (1) or 60-50° (2)	ca. 80-70°								
Angle of ascending ramus for tooth row										
Lower dental characters										
Lower dental characters	Trogonus				Kuanchuanius		Higotherium		Chungchienia	
	Trogosus	Tillodon	Retained	Lost	Retained	Yes	?	?	?	?
1/1 and 1/3	Retained	Lost								
Longitudinal groove on 1/2 labial surface	No	No								
Space between cheek teeth	Loose (1) or crowded (2)	Much crowded								
Diastema before P/3	Relatively long (1) or short (2)	Long								
P/4	Submolariform	Less molariform								
Crown of molars	High	Low								
Buccal enamel surface of molars rugose	No	No								
M/3 metaconid	Somewhat elongated	Less elongated								
M/3 metastylid	Prominent	Weak or lost								
M/3 talonid basin apparently divided	Yes (3) or no (4)	?								
Presence of M/3 mesoconid	?	?								
Additional cusp on M/3 paracristid	No	No								
M/3 precingulid	Reduced or lost	Reduced or lost								

whereas the M/3 buccal wall is much less so or not convex (Figures 5D and 6D). These features are unshared with *H. hypsodon*. In addition, in IVPP V 2764 all cusps on the molars are less developed; especially the M/3 metaconid is more slender; all ridges are narrower; and on M/3 a mesoconid is never recognized. However, *K. shantunensis* possesses a few similar accessory cusps on the molars; the broken M/3 third lobe has a hint of forming a small enclosed basin with a low posthypocristid as in *T. grangeri*; and a sharp precingulid obviously exists in both M/2 and M/3 (Figure 5D).

Chungchienia Chow, 1963: Chow *et al.* (1996) recently reexamined the systematic position of *Chungchienia* Chow, 1963b, and concluded that it is the most derived and gigantic genus of tillodonts, with an extremely deeper mandible and highly specialized teeth. All known lower cheek teeth of *Chungchienia* are rootless with enamel covering restricted to the buccal side (Chow *et al.*, 1996). This Chinese genus includes two species: *C. sichuanica* Chow, 1963b (type species) and *C. lushia* Chow *et al.*, 1996. As Chow *et al.* (1996) mentioned, *Chungchienia* was previously believed to be an edentate or taeniodont until a new huge species, *C. lushia*, was described.

Higotherium differs from *Chungchienia* in having a shallower mandible, less hypsodont cheek teeth with lingual enamel covering, and an anteroposteriorly shortened M/3 third lobe (Tables 1 and 2). The extremely hypsodont teeth of *Chungchienia* suggest that the mandible of *Chungchienia* was much deeper than that of *Higotherium*. The depth of the mandible is over 60 mm in *C. sichuanica* (IVPP V 2767; Chow, 1963b), and the depth is estimated to have been over 80 mm in *C. lushia* (IVPP V 10805), although the mandible of *C. lushia* has never been found. Individual cusps of the lower molars of IVPP V 10805 are not observed because of the heavy wear; the presence of precingulids of the molars is also unknown in *Chungchienia*. However, in *Chungchienia* the buccal enamel surfaces of the cheek teeth are markedly rugose with longitudinal fine lines (see also Chow *et al.*, 1996 and Chow, 1963b). The lower molars of *Higotherium* also possess a similar rugose enamel surface on the buccal side.

Discussion

Dental characters of *Higotherium*: Compared with *Kuanchuanius*, *Trogosus*, and *Tillodon*, *Higotherium* apparently possesses much more hypsodont molars with additional accessory cusps, but it is not so highly specialized as *Chungchienia*. In the first three genera, cervical lines are observed on lower molars above the dentary; in *Higotherium* the cervical lines are unexposed in spite of the fully erupted (M/2) and considerably erupted (M/3) crowns; this enamel extension into the dentary in *Higotherium* indicates a higher degree of hypsodontology. Moreover, the eruptional stages and wear patterns of *Higotherium* apparently differ from those of *Kuanchuanius*, *Trogosus*, and *Tillodon*: the M/3 eruption is much later than that of M/2 in *Higotherium*, and the M/3 talonid never sufficiently erupted to chew in this stage. The higher degree of hypsodontology and the delayed eruption of

M/3 relative to M/2 are both among evolutionary patterns related to the elongation of the tooth wear as seen on various other mammals. In addition, the presence of an additional small cusp on the M/3 paracristid is unknown in previously described tillodonts. The high-crowned M/3 third lobe of NSM-PV 20118 forms a complete, enclosed basin, but it is anteroposteriorly shortened. The short M/3 third lobe is extraordinary in Trogosinae. The lack of elongation of the M/3 third lobe may be interpreted as a pathologic feature, although Gazin (1953, p. 68) noted the variability of development of a third lobe in M/3 of *Trogosus*; however, we do not have sufficient evidence to consider this as a pathologic feature. On the other hand, presence of precingulids in *Kuanchuanius* and *Higotherium* can be interpreted as a vestigial feature for trogosines since the more primitive taxa (e.g., *Esthonyx* Cope, 1874, *Plesiasthonyx* Lemoine, 1891, and *Franchiaius* Baudry, 1992) also have sharp precingulids on their lower molars, whereas in *Trogosus* and *Tillodon* precingulids are almost completely reduced or lost, as mentioned in the previous section.

Trogosine monophyly and phylogenetic position of *Higotherium*: Previously proposed phylogenetic hypotheses among Tillodontia (e.g., Stucky and Krishtalka, 1983; Baudry, 1992; Lucas, 1993) verify the monophyly of Trogosinae, but raise a few arguments and problems. As for trogosine monophyly, it is difficult to assess the precise phylogenetic relationships within trogosines because of the incompleteness of Asian material (Lucas, 1993). Therefore, the comparative characters which support the interrelationships are based mostly on the mandible and lower dentition, and the upper dental character states suggested by nodes 9 and 10 of Lucas (1993) should be viewed as provisional, until other characters become established in Asian trogosines.

We believe the subfamily Trogosinae is a monophyletic group composed of five valid genera: *Trogosus*, *Tillodon*, *Kuanchuanius*, *Higotherium*, and *Chungchienia* (see also Figure 7). Based on our reexamination, these five genera share the following synapomorphies: elongated rootless I2/2 (*), much deepened mandible with posteriorly extending symphysis at least under P/4 talonid (*), distinctly hypsodont lower cheek teeth with developed cusps and ridges, and basin-shaped M/3 third lobe (node 1 in Figure 7), although definitive data on characters with asterisks (*) are absent for *Higotherium*. Some of these are modified from the previous hypotheses (i.e., node 7 of Stucky and Krishtalka, 1983; node 9 of Lucas, 1993), but all character states support trogosine monophyly. However, single-rooted P/2 represented by Stucky and Krishtalka (1983) is no longer a synapomorphy of Trogosinae, since this character occurs in some other tillodonts: *Esthonyx spatularius* Cope, 1880, *Azygonyx gunnelli* Gingerich, 1989, *Megalesthonyx hopsoni* Rose, 1972, and probably *Basalina basalisensis* Dehm and Oettingen-Spielberg, 1958 (Gingerich and Gunnell, 1979; Lucas and Schoch, 1981). Moreover, reduction of C, P/2, and talonids on P/3–4 are plesiomorphic for trogosines because these characters also occur in *Megalesthonyx hopsoni*.

Lucas (1993) proposed a broader conception of Trogosinae which include *Megalesthonyx* Rose, 1972 and

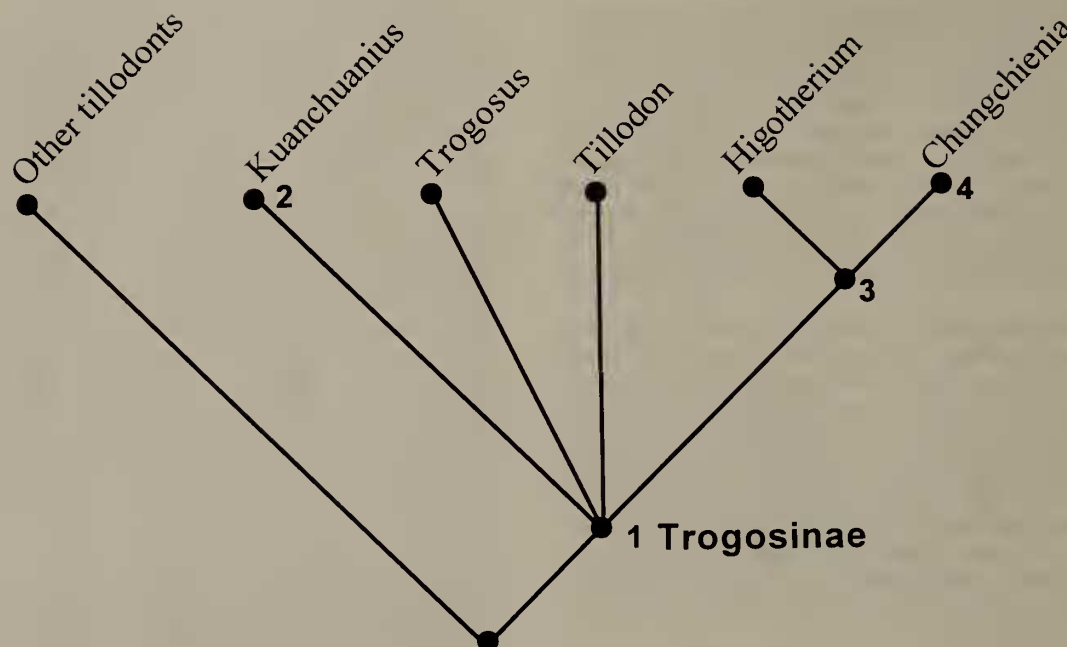


Figure 7. A phylogenetic hypothesis among Trogosinae. **Node 1:** elongated rootless I2/2, much deepened mandible with posteriorly extending symphysis at least under P/4 talonid, distinctly hypsodont lower cheek teeth with developed cusps and ridges, basin-shaped M/3 third lobe; **node 2:** presence of a longitudinal groove on labial surface of I/2; **node 3:** much more hypsodont molars with expanded enamel extending into dentary; **node 4:** gigantic body size, extremely deeper mandible, further reduction or loss of talonids on P/3 and/or P/4, elongated rootless cheek teeth without lingual enamel layer.

Adapidium Young, 1937, using criteria other than I2/2 morphology (Chow *et al.*, 1996). Although these two taxa possess a few derived trogosine dental characters (e.g., cristid obliqua close to metaconid; see nodes 6 and 7 of Lucas, 1993), it is questionable whether *Megalestonyx* and *Adapidium* should be included in Trogosinae since synapomorphies of the traditional classification of Gazin (1953) and Rose (1972) are absent or unestablished. We do not readily accept Lucas's taxonomic suggestion since these two taxa possess none of the synapomorphies we list above.

As the tetrachotomy in Figure 7 shows, it is difficult to resolve the phylogenetic relationships among *Kuanchuanianus*, *Trogosus*, and *Tillodon* at present. Lucas (1993) reassigned *Kuanchuanianus* as a junior synonym of *Trogosus*, and other authors (Stucky and Krishtalka, 1983; Baudry, 1992; Chow *et al.*, 1996) suggested that *Kuanchuanianus* may be a questionable taxon among the trogosine monophyletic group. Actually, *K. shantunensis* is similar to the "short-faced" *Trogosus* species (*T. castoridens* and *T. hillsii*) in its mandibular size and morphology. The slender cusps, sharpened ridges on the molars, and short diastema between P/2 and P/3 may also indicate that *Kuanchuanianus* is morphologically primitive, close to a common ancestor of all other trogosines, as Stucky and Krishtalka (1983, p. 389) mentioned. However, *Kuanchuanianus* also possesses peculiar I/2 characters which were already pointed out by Chow (1963a): the I/2 is oval in cross section, and a shallow but marked groove runs

longitudinally on the labial enamel surface (node 2 in Figure 7). The former condition may be interpreted as primitive among trogosines, but the latter condition is probably an autapomorphy based on our reexamination.

Tillodon possesses many derived characters (e.g., somewhat broad and long rostrum, long diastema between P/2 and P/3, loss of I/1 and I/3, less molariform P/4, and smaller M3/ than M2/) in comparison with *Trogosus* and *Kuanchuanianus*. However, we can not identify what are its own autapomorphies and synapomorphies shared with other genera among these character states. Chow *et al.* (1996) concluded that *Chungchienia* is more similar to *Tillodon* than *Trogosus* and *Kuanchuanianus* in having the following three aspects: a greatly elongate rostrum suggested by the large second incisor, much longer diastema before P/3, a narrow M3/ reflected by the narrow M/3. These derived similarities seem reasonable to infer close relationships between these two genera, but it is disputable to regard these as synapomorphies shared only with *Tillodon* and *Chungchienia*. For example, *Trogosus grangeri* also possesses a relatively long diastema between P/2 and P/3; and another example, if the posteriorly narrower M/3 undoubtedly reflects that M3/ is narrower (smaller) than M2/, *Kuanchuanianus* also shares this feature. Furthermore, the lower cheek teeth of *Tillodon* are relatively brachydont with bulbous cusps in spite of its large body size, and this conflicting character does not support close relationship with *Chungchienia*. The dental mor-

phological gap between *Chungchienia* and the other previously described genera is very broad.

Higotherium is more derived than *Kuanchuanius*, *Trogosus*, and *Tillodon* in having much more hypsodont molars. The possession of expanded enamel extending into the dentary (=higher degree of hypsodonty) indicate that *Higotherium* is phylogenetically and morphologically closer to *Chungchienia* than to the three other genera (node 3 in Figure 7). However, the two additional M/3 accessory cusps in *Higotherium* cannot be demonstrated to be its own autapomorphies until the detailed features of cusp patterns in other genera are better established. In any case, *Chungchienia* is the most derived trogosine in having the following autapomorphies (node 4 in Figure 7): extremely deeper mandible due to its gigantic body size, further reduction or loss of talonids on P/3 and/or P/4, and elongated rootless cheek teeth without lingual enamel layer (Chow *et al.*, 1996).

Our hypothesis of phylogenetic relationships among the trogosines leaves room for a variety of interpretations; for example, it is possible that almost all generic diversification within Trogosinae occurred in Asia, and North American trogosines were immigrants or descendants of immigrants from Asia as Stucky and Krishtalka (1983) pointed out. According to Stucky and Krishtalka (1983) and Krishtalka *et al.* (1987), *Trogosus* has been known only from the Bridgerian (late Early to early Middle Eocene; Prothero, 1995) of North America. Its first appearance, together with certain other taxa such as *Palaeosyops* and *Hyrachyus*, identifies the beginning of the Bridgerian (Krishtalka *et al.*, 1987; Gunnell *et al.*, 1992). *Tillodon* is also recorded from the Bridgerian (Krishtalka *et al.*, 1987: 88), although known occurrences of *Tillodon* are very rare. In China, *Kuanchuanius shantunensis* and *K. ? danjiangensis* are known from the Guanzhuang Formation, Xintai Basin, and the lower part of Dacangfang Formation, Liguangqiao Basin, respectively. These two formations of China are correlated with the Bridgerian land mammal age of North America based on the mammal fauna (Tong, 1989). *Chungchienia* is known from Middle Eocene strata of China (Chow, 1963b; Chow *et al.*, 1996): the Hetaoyuan Formation in Liguangqiao (=Xichuan) Basin (*C. sichuanica*) and Lushi Formation in Lushi Basin (*C. lushia*); these two formations are slightly younger than the Guanzhuang Formation according to Tong (1989). These occurrences, in addition to the occurrence of *Higotherium*, indicate that the rapid generic diversification of trogosines occurred slightly before and during the Middle Eocene. It is most likely that Early Eocene tillodonts from Asia are very important keys for trogosine origins although to date none have been found.

Acknowledgments

We thank Richard H. Tedford and John P. Alexander (AMNH), Mary A. Turner and Christine L. Chandler (YPM), Robert J. Emry and Robert W. Purdy (USNM), and Li Chuan-kuei (IVPP) for permission and assistance to examine comparative specimens. We also wish to express our gratitude to Everett H. Lindsay (University of Arizona) and Kenneth D. Rose (Johns Hopkins University) for reading the manuscript

and making a number of helpful suggestions. Many helpful comments for this research were given by Teruya Uyeno, Makoto Manabe, Naoki Kohno (NSM), and Yasuhide Iwasaki (Kumamoto University, Ph.D. supervisor of K. M.). Makoto Manabe also helped us to take radiographs in this research. This research was supported in part by a grant from Fujiwara Natural History Foundation, Tokyo, Japan.

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